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The effects of the spreading of the Central Atlantic during the Middle Jurassic on dinosaur faunas

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Abstract

The spreading of the Central Atlantic is a complex series of events that include a ridge jump to the east and a ridge jump to the west at c. 170Ma and c. 162Ma respectively. These jumps were influenced by plate interactions as Laurasia separated from Gondwana, although the second jump may have been influenced by spreading in the Gulf of Mexico, which occurred at about the same time. Dinosaur evolution and diversity were influenced by the spreading of the Central Atlantic that split Laurasia from Gondwana. The presence of dinosaurs, from the same taxonomic groups existed in the two regions from the Triassic until the Early Cretaceous, suggests that there continued to be at least some mixing between Laurasian and Gondwanan faunas. This may have been due to the proximity of the continents during the early stages of opening of the Atlantic, island hopping, or other means, enabling limited contact between Laurasia and Gondwana throughout the Mesozoic. Dinosaur faunas did, however, become more isolated and diverse later, in the Cretaceous, due to higher sea levels and seafloor spreading, but some elements of the faunas were still common to both continents. Similarities in faunas between North America and Asia, suggest that there were still links between these regions until the Maastrichtian at the end

of the Late Cretaceous. In Laurasia some apparently endemic dinosaur groups (ceratopsians, pachycephalosaurs, therizinosaurs and others) developed as a result of the break up of the continents and do not seem to have had any contact with Gondwana.

The diversity of dinosaurs has some differences between Laurasia and Gondwana from the Late Jurassic onwards. During the Cretaceous, Laurasian hadrosaurs and ceratopsians dominated the herbivores. Both these groups of ornithischian dinosaurs were able to chew their food, which aided their ability to digest tough vegetation making it possible for them to evolve to be much smaller in size than their Gondwanan counterparts, the titanosaurid sauropods — a surviving group of the giant saurischian herbivores characterised by their inability to chew and by their enormous size.

There is also always the possibility that the apparent differences between the faunas are due to collecting bias and to differences in outcrop exposure in the present-day remnants of these once vast continents. There are certainly a lot fewer localities in the land masses that made up Gondwana as compared to Laurasia.

Introduction

Plate movements in the Central Atlantic

A great deal has been written on the development of the spreading ridge in the North, Central and South Atlantic that split Laurasia from Gondwana. The Gulf of Mexico basin began to form in the Late Triassic as a result of rifting within Pangaea along zones of weakness in the crust, perhaps relating to the lines of collision existed during the formation of Pangaea in the Palaeozoic. Some have speculated that the rifting may have been the result of an extraterrestrial impact, but few geologists support this hypothesis (Stanton 2002; Mickus *et al.* 2009). The relative motions of the continents have been calculated by many authors, reconstructing the plate movements using the geomagnetic isochrons (M0, M25 and M40) for the Early Aptian, Kimmeridgian and Late Bathonian, respectively (Bird and Burke 2006; Bird *et al.* 2007) (Fig. 1, *overleaf*). The Jurassic Magnetic Quiet Zone (JMQZ) is about 70km wider in the African JMQZ than in the corresponding area in the North American JMQZ. This suggests that there was a shift in the spreading ridge to the west between isochrons M38 and M32 (164–159 million years ago) soon after spreading began in the Central Atlantic, and appears to coincide with spreading in the Gulf of Mexico and a reorganisation of the positions of the North American and Gondwanan plates (Bird *et al.* 2007).

Between M40 and M25, the Yucatan block appears to have rotated c. 22° anticlockwise. This, coupled with the crustal stretching and thinning, opened the subsiding basin to flooding from the Pacific Ocean across central Mexico. The restricted nature of the basin allowed salt deposition over large areas of continental shelf during the Middle Jurassic (Hall and Najmuddin

1994). Between M25 and M0 there was a further rotation, of c. 20° anticlockwise, associated with the completion of the formation of the Gulf of Mexico. During the Late Jurassic continued rifting had widened the Gulf of Mexico sufficiently, and opened the Atlantic Ocean enough, to allow adequate circulation, that halted salt deposition.

Sea floor spreading appears to have been initiated by a lithospheric plate event (or mantle plume in the form of a hot spot) beneath the Gulf of Mexico (Bird *et al.* 2005; Bird and Burke 2006). About 170 million years ago there was a shift of the spreading ridge to the east by about 90km (Vogt *et al.* 1971). This was followed 10 million years later by a further 35km shift to the west, which coincided with the rotation of the Yucatan and the formation of the Gulf of Mexico (Buffler and Thomas 1994; Hall and Najmuddin 1994).

The chronology of the break-up of Pangaea and the formation of the Atlantic Ocean is summarised as follows (Bird and Burke 2006):

Triassic (250–206 million years ago)

- 230 million years (Ma) Pangea breakup began
- 230 to 164Ma Plate subduction in western Mexico and stretching of the Yucatan block

Early Jurassic (206–180 million years ago)

- 200Ma Central Atlantic Magmatic Province (CAMP) lithospheric plate event erupts
- 180Ma Seafloor spreading began in the Central Atlantic (Withjack *et al.* 1998)

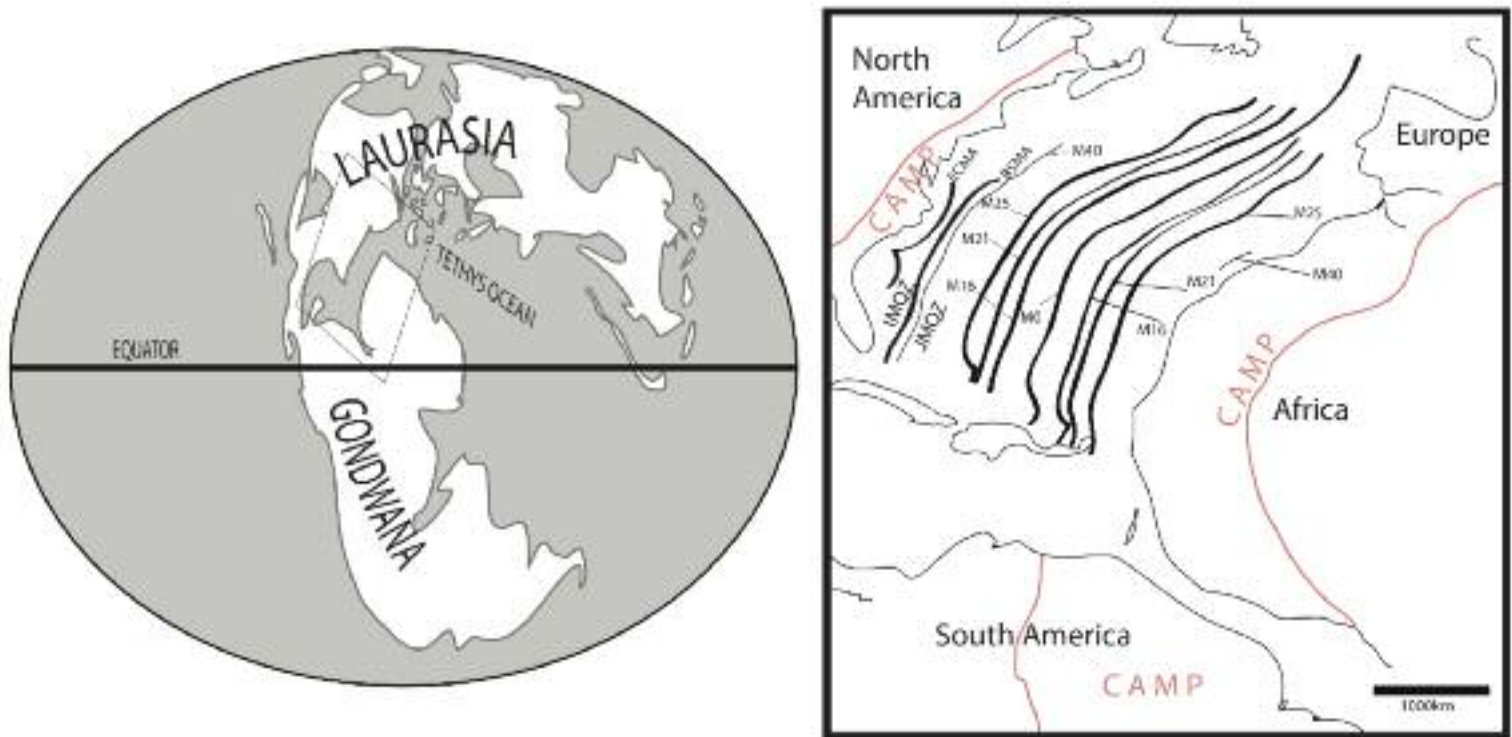


Figure 1 (left) A reconstruction of the positions of the continents during the Middle Jurassic (170 million years ago — based on global reconstructions by Blakey 2011); (right) Early Cretaceous (M0 = 120 million years ago) reconstruction showing geomagnetic isochrones M16 (138 million years ago; Early Cretaceous), M21 (147 million years ago; Tithonian, Late Jurassic), M25 (154 million years ago; Kimmeridgian, Late Jurassic) and M40 (167 million years ago; Bathonian, Middle Jurassic). JMQR = Jurassic Magnetic Quiet Zone; IMQR = Inner Magnetic Quiet Zone; BSMA = Blake Spur Magnetic Anomaly; ECMA = East Coast Magnetic Anomaly; CAMP = Central Atlantic Magmatic Province (based on Bird et al. 2005b, and McHone nd).

Middle Jurassic (180–159 million years ago)

- 170Ma Eastward ridge jump in the Central Atlantic (abandoning African lithosphere on the western flank) (~M40)
- 160Ma Westward ridge jump in the Central Atlantic (abandoning North American lithosphere on the eastern flank) (M32–38)
- ~160Ma Yucatan block began to rotate away from North America, 24° counter-clockwise continental extension (~M32)

Late Jurassic (159–145 million years ago)

- ~150Ma Seafloor spreading in the Gulf of Mexico, 20° anti-clockwise rotation of the Yucatan block (M22–23)

Cretaceous (145–65 million years ago)

- ~140Ma Gulf of Mexico formation was complete (M17)
- ~126Ma South America began separating from Africa (M3–4)

Dinosaur distribution

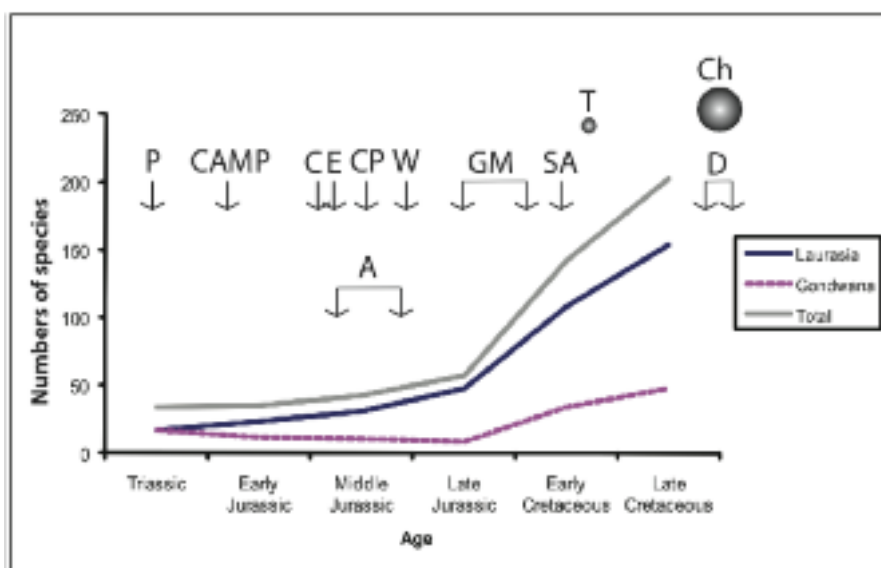
There are only a handful of Triassic dinosaur localities around the world and not very many specimens either (except in particular localities, such as in the Chinle Formation in Arizona, from which several hundred complete individuals of *Coelophysis* have been collected). This makes it difficult to compare the distribution of dinosaur groups of this age around the world in a meaningful way. As a whole, dinosaurs are probably not the best choice of living organism for looking at the relationship between the split of Pangaea and endemism, as these are generally large animals with a poor fossil record — although this is improving each year, and the more we find, the better our understanding of this relationship will become. It is not their size that affects their endemism, but their size does affect their fossil record, as large animals are often

missed in small excavations. The dinosaur fossil record is particularly poor from the Triassic, and the Middle Jurassic, from which few dinosaur species are known (Fig. 2, *opposite*).

To look for changes in dinosaur distribution as a result of the opening of the Central Atlantic during the Middle Jurassic, it is necessary to look at dinosaur distribution throughout the time span of dinosaur existence, excluding those that survived the end-Cretaceous extinction.

It is generally thought that there were several groups of dinosaurs that evolved in isolation — such as the therizinosaurs of Asia, and pachycephalosaurs of North America), or even migrated to different parts of the World at different times (such as some sauropods and thyreophorans — and that this may reflect particular events in the tectonic, sea-level and climatic history of the Earth (Holtz et al. 2004). It is difficult, therefore, to know whether the absence of a particular group of dinosaurs is because it was never there, or just has not yet been discovered. In other words: can the absence of evidence be taken as evidence of absence? It is also not certain where the majority of coastlines were at any particular time. We may know with a degree of certainty where the continents were relative to each other, but not the extent to which they were covered by water and for how long. During the Middle Jurassic, for example, there was a huge continental sea in North America in which dinosaur footprints were discovered. These dinosaurs were walking on the sediment surfaces some distance seaward of the supposed shoreline (Clark and Brett-Surman 2008). This, of course is impossible unless there were major, short-lived regressions during the time of the inland sea. Shorelines and land bridges are not easily determined with precision.

Figure 2 Graph showing the number of species of dinosaurs from the Late Triassic to the Late Cretaceous for Laurasia and Gondwana, as well as volcanic and tectonic activity, and large bolide impacts. (P = Pangaea begins to split; CAMP = Central Atlantic Magmatic Province; C = Central Atlantic seafloor spreading begins; E = Eastward ridge jump; CP = Circum-Pacific volcanism; W = Westward ridge jump; GM = Gulf of Mexico seafloor spreading; SA = South Atlantic opens; D = Deccan lavas erupt; A = Antarctic volcanism; T = Tookoonooka impact; Ch = Chixulub impact.



Methods

The distribution data for dinosaurs was obtained from the global list of dinosaurs produced by Weishampel *et al.* (2004b) with the addition of further more recent examples of Scottish dinosaurs (Clark 2007; Gilchrist 2008). The dinosaur groups used in this study are as follows:

Ornithischia

Ankylosauria
Basal Ornithischia
Basal Thyreophoran
Centrosaurinae
Ceratopsia
Chasmosaurinae
Dryosauridae
Euhadrosauria
Euornithopoda
Hadrosauridae
Heterodontosauridae
Iguanodontia
Lambeosaurinae
Nodosauridae
Pachycephalosauria
Stegosauria

Saurischia

Allosauroidae
Avialae
Basal Saurischia
Brachiosauridae
Camarasauridae
Carcharodontosauridae
Carnosauria
Coelophysoidea
Coelurosauria
Dromaeosauridae
Eusauropoda
Herrerasauridae
Lithostrotia
Micronaria
Neoceratosauria
Neosauropoda
Ornithomimosauria
Oviraptorosauria
Prosauropoda
Saltasauridae
Sauropoda
Spinosauridae
Tetanurae
Therizinosauroidea
Titanosauria
Troodontidae
Tyrannosauroidea

The numbers of genera present during the major subdivisions of the Mesozoic were counted. Data for the Triassic, Early Jurassic, Middle Jurassic, Late Jurassic, Early Cretaceous and Late Cretaceous were recorded for each present-day continent and then combined to provide the listings for the northern continents

(Asia, North America, Europe) representing Laurasia, and the southern continents (South America, Africa, India, Australasia and Antarctica) representing Gondwana.

The data from the present-day continents were added together in this way to reflect the Mesozoic distribution of the continents and to identify any potential links between the two major continents at that time. North American faunas were also compared with Asian faunas to see if it was possible to determine the timing of the opening of the northern Atlantic basin. In addition, the Middle Jurassic and Late Jurassic were further split into their respective stages from the Aalenian to the Tithonian and the number of species, localities and formations were counted to provide a more detailed distribution at the time the Central Atlantic was opening using Weishampel *et al.* (2004a) and Clark (2007).

The data were graphically represented in order to visually identify any possible changes in the presence of the above dinosaur groups across the Mesozoic continents.

Results by age

Late Triassic (227–206 million years ago)

During the Carnian to Rhaetian dinosaurs first appeared. Only a few groups of dinosaurs are represented during the Triassic, but the faunas do not appear to be very different between the northern continent (Laurasia) and the southern continent (Gondwana), which developed as a result of the opening of the Atlantic and Tethys seas (Fig. 3A, *overleaf*). In other studies by Holtz *et al.* (2004) — using the same data in a phenetic dinosaurian distribution analysis study with precise locality information for 238 sites as well as 77 distinct taxa — noted the cosmopolitan nature of the distribution of herrerasaurids, coelophysoids, prosauropods and basal ornithischians from the Late Triassic to the Early Jurassic. This agrees with the current study's assertion that the faunas are similar between the Gondwanan and Laurasian regions early in the Mesozoic.

Early Jurassic (206–180 million years ago)

From the Hettangian to the Toarcian, there does appear to be some differences between the faunas in the regions that were to become Laurasia and Gondwana, with some groups surviving one area and not the other, as well as some new taxa appearing (Fig. 3B). In the Laurasian region, basal thyreophorans, neo-

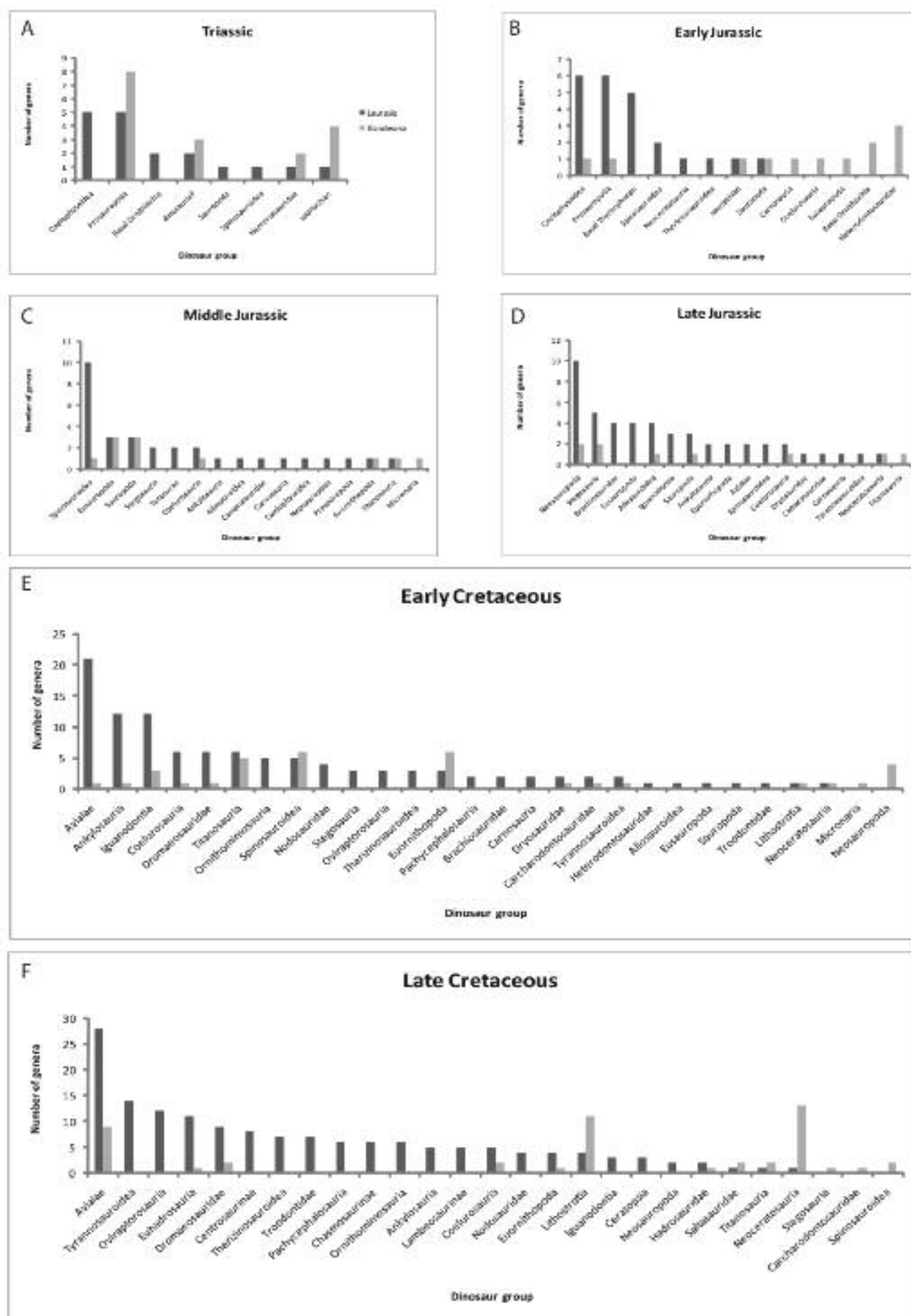


Figure 3 (opposite page) A series of graphs showing the changes in dinosaur generic abundance of various groups from the Triassic to the Late Cretaceous for Laurasian (dark grey) and Gondwanan (light grey) faunas: A Triassic; B Early Jurassic; C Middle Jurassic; D Late Jurassic; E Early Cretaceous; F Late Cretaceous.

ceratosaurians and therizinosauroideans first appear, and in the Gondwanan region, some basal ornithischians survive and heterodontosaurs, carnosaurs, coelurosaurs and eusauropods first appear (Fig. 4). The other taxa appear to be cosmopolitan: the coelophysoideans, prosauropods, basal saurischians and the sauropoda. This agrees broadly with Holtz *et al.* (2004), if the heterodontosauridians and basal thyreophorans are included in the basal ornithischians, who noted that there remained a similarity in the faunas into the Lower Jurassic.

Middle Jurassic (180–159 million years ago)

This is the time in which the Central Atlantic is opening, beginning 180 million years ago, as well as the east and west jumps of the Atlantic ridge, circum-Pacific volcanism and extensive Antarctic volcanism. There is a broad correlation of taxa between the northern and southern continental regions from the Aalenian to the Callovian (180–159 million years ago) (Fig. 3C) and only one group of dinosaurs unique to Gondwana — the Micronaria. The differences between Laurasian faunas and Gondwanan faunas include several new taxa such as the Ankylosauria, the Stegosauria, the Tetanurae, the Allosauroidae, the Camarasuridae and the Neosauropoda, in the north and as well as the Micronaria in the south (Fig. 3C). There are also new taxa common to both continents, suggesting that there was at least some communication between faunas: the Euornithopoda and the Titanosauria. The larger number of dinosaur groups represented in the Laurasian region may be an effect of the smaller number of dinosaur-bearing localities in the Gondwanan region (less than 20%).

Holtz *et al.* (2004) noted that there were faunal differences between Europe, Asia and North America plus Africa. It should also be noted that there was a difference between the Asian faunas and North American faunas in the Early Jurassic, as well with only two out of the five taxonomic groups represented in both regions (the basal thyreophorans and the prosauropods).

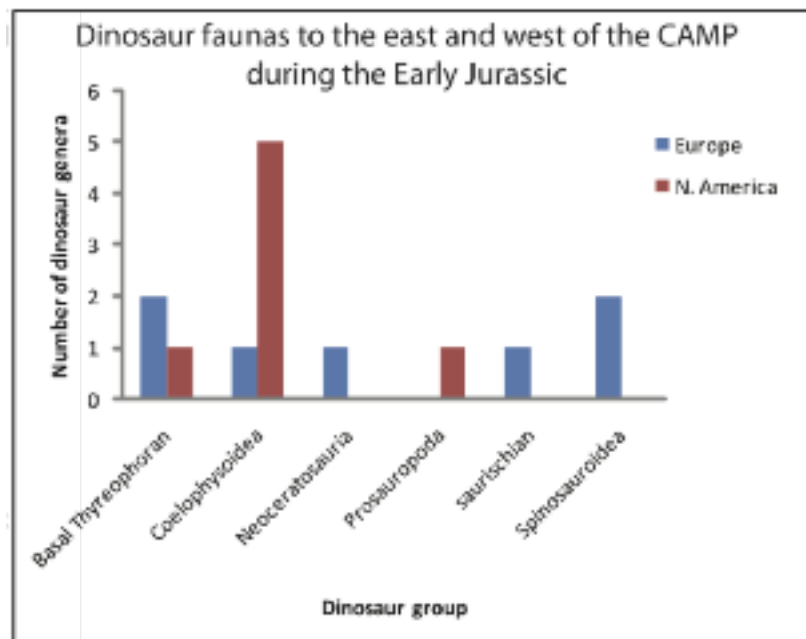
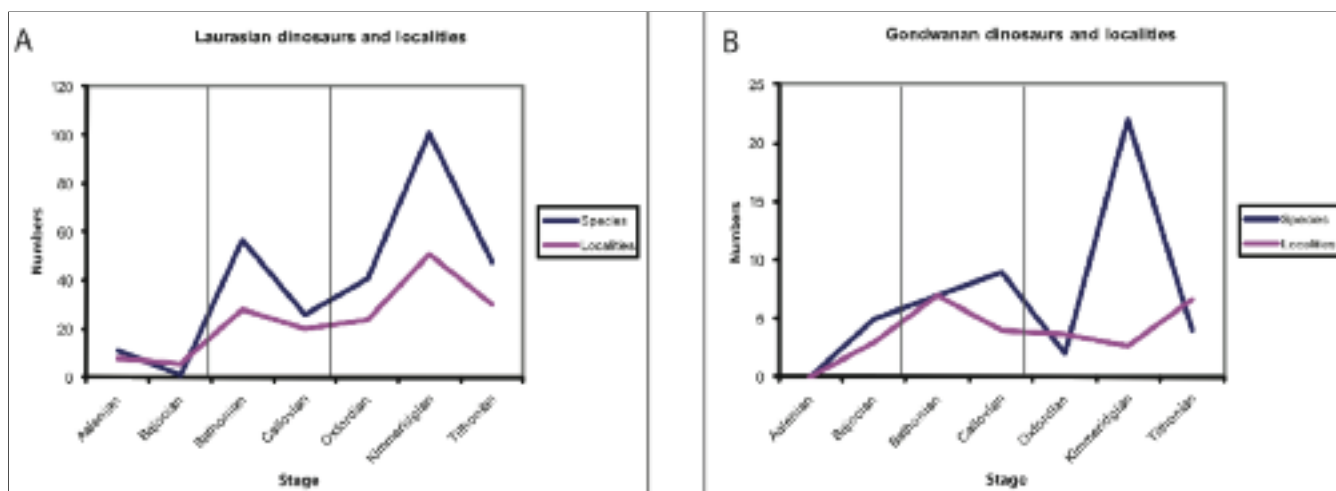


Figure 4 (right) Comparison of faunas to the west (North America) and east (Europe) of the CAMP (Central Atlantic Magmatic Province) in the Early Jurassic.

There are fewer Middle Jurassic dinosaur localities worldwide than there had been prior to and after that time, with less than 20% of the localities than in the Lower Jurassic. This may have been due to fewer discoveries rather than to fewer dinosaurs. However, when the data are looked at for species and localities in the Middle Jurassic by stage, there is greater variation in the numbers of species at different times than in the number of localities (Fig. 5A and B). The number of dinosaurs tends to increase with an increase in the numbers of dinosaurs-bearing localities by a factor of nearly two. Other factors, such as the amount of exposure of rocks of the right age or environment will also have an effect and are beyond the scope of this study. The Kimmeridgian peak is lacking from the locality profile in the Gondwanan faunas, suggesting a genuine increase in species numbers (Fig. 5B), i.e. the increase in species is not due to the increase in the number of localities. The small number of localities in Gondwana at this time, however, makes it difficult to draw too many conclusions about this relationship.

As most of the localities and species of dinosaurs are found in Europe, these were removed to see if that would affect the correlation

Figure 5 Graphs showing the number of species found at different stages of the Middle and Late Jurassic in Gondwana (A), and Laurasia (B). Vertical lines represent the ridge jumps to the east (left) and to the west (right).



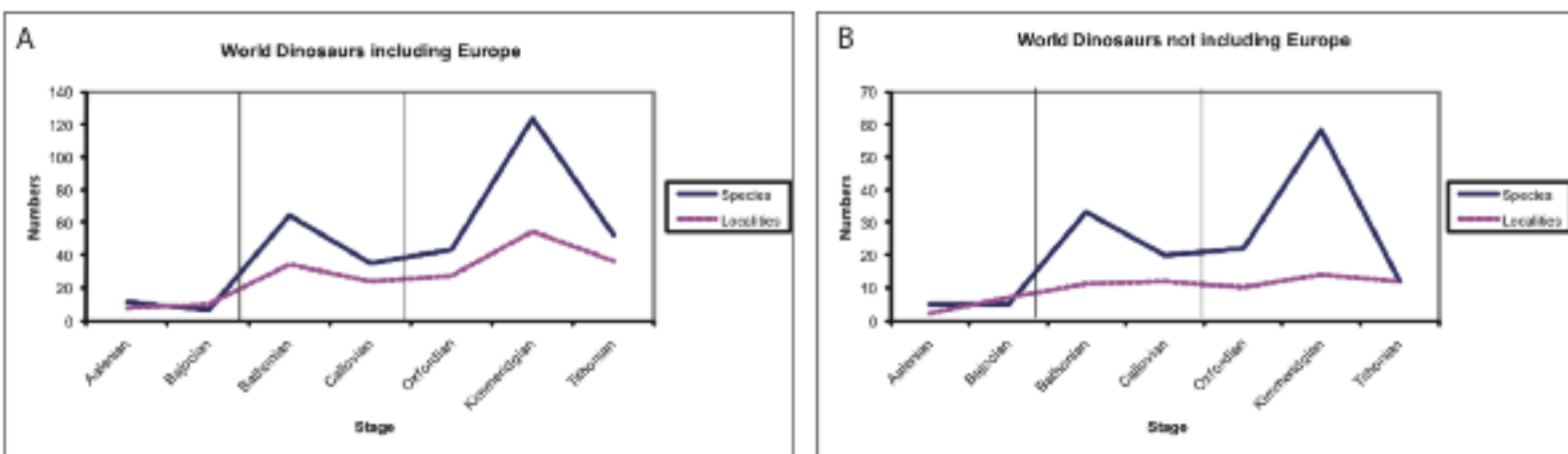
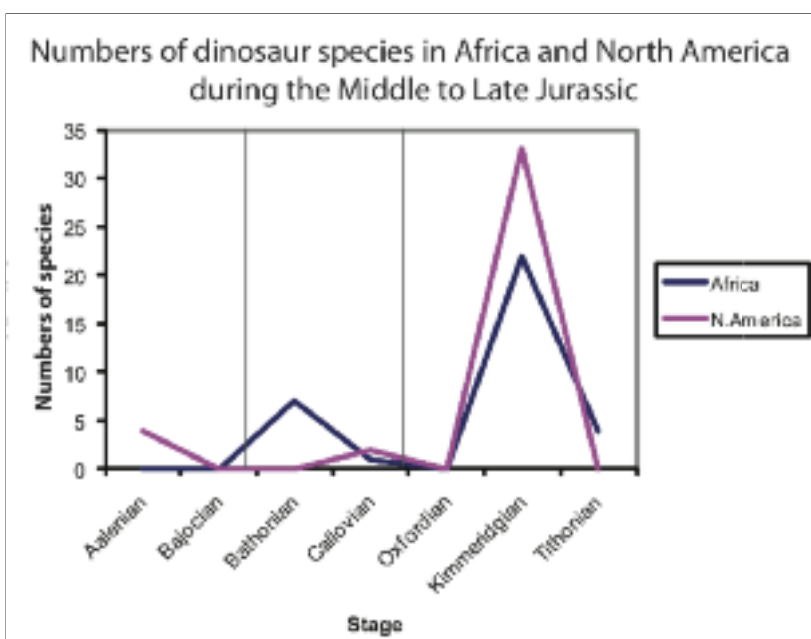


Figure 6 Graphs showing the global number of dinosaur species with the number of localities during the Middle to Late Jurassic (A) and with European data extracted (B). Vertical lines represent the ridge jumps to the east (left) and to the west (right).

between numbers of species with stage (Fig. 6A and B). The resultant graph shows the same two peaks with a dip in the Callovian and Oxfordian and a further reduction in species number in the Tithonian. The localities profile is almost the same as that of the species number profile for the Laurasian faunas including Europe, but the Kimmeridgian localities peak is less pronounced in the Laurasian faunas not including Europe. This supports the idea that the dinosaur numbers may be affected by contemporaneous events rather than being an artefact of the data.

When the African and North American faunas, which are most likely to be affected by the Central Atlantic spreading event due to their proximity to the spreading ridge, are looked at in isolation, the curves match closely (Fig. 7). Although no dinosaur remains are recorded from North America during the Bathonian, and only a few from the rest of the Middle Jurassic, there is plenty of evidence to show the presence of sauropod, ornithomimid and theropod dinosaurs from their tracks at 13 localities in the United States and Mexico during the Middle Jurassic (Weishampel *et al.* 2004a).

Figure 7 Graph showing data for African and North American dinosaur species during the Middle to Late Jurassic. Vertical lines represent the ridge jumps to the east (left) and to the west (right).



Late Jurassic (159–145 million years ago)

There is a similarity between the Gondwanan and Laurasian faunas, but there are a lot more groups represented in the northern continent than in the south during the Late Jurassic (Fig. 3D). The main differences are with the types of sauropods: eusauropods, camarasaurids and brachiosaurids in the Laurasia; and titanosaurs in the Gondwana, with neosauropods common to both regions. Ornithomimids such as dryosaurs, euornithomimids and iguanodonts are also found only in the Laurasian region. The carnivorous saurischians of Laurasia include primitive birds (Avialae), spinosaurs and tyrannosaurs. Due to the very low number of dinosaurs in the southern continent at this time, it is difficult to draw too many conclusions from this as there are only a few localities presently known in the Gondwanan region.

There are a few groups that seem to survive and flourish during the Tithonian. Stegosaurids increase from six species in the Kimmeridgian to eight species in the Tithonian, neosauropods lose one species from 14 to 13 and tyrannosaurids stay level at one species, but survive well into the Cretaceous (Fig. 8, *opposite*).

Cretaceous (145–65 million years ago)

Although the number of known localities increases substantially for the Cretaceous, the number of Gondwanan localities increases only slightly compared to those of the Laurasian continental region and represents only about a quarter of the Laurasian localities. This is reflected in the numbers of dinosaur species as well as by the fact that there are only a third of the number of species represented in the southern continent in the Early Cretaceous (145–100 million years ago) and less than a fifth in the Late Cretaceous (100–65 million years ago) (*see* Fig. 2). Most groups seem to be present in both Laurasia and Gondwana, but there are a few dinosaur groups that appear endemic to the Laurasian faunas especially in the Late Cretaceous (Fig. 3E and F). However, nodosaurids, iguanodonts, lambeosaurids, pachycephalosaurids, ceratopsians, therizinosaurs and troodontids seem to be present only in the northern continental region. In the southern regions, spinosaurs, carcharodontosaurus, and stegosaurs survive into the Late Cretaceous after becoming extinct in the north. Titanosaurs were essentially Gondwanan, although a few seem to have been able to island-hop to southern parts of Laurasia, perhaps from northern Africa

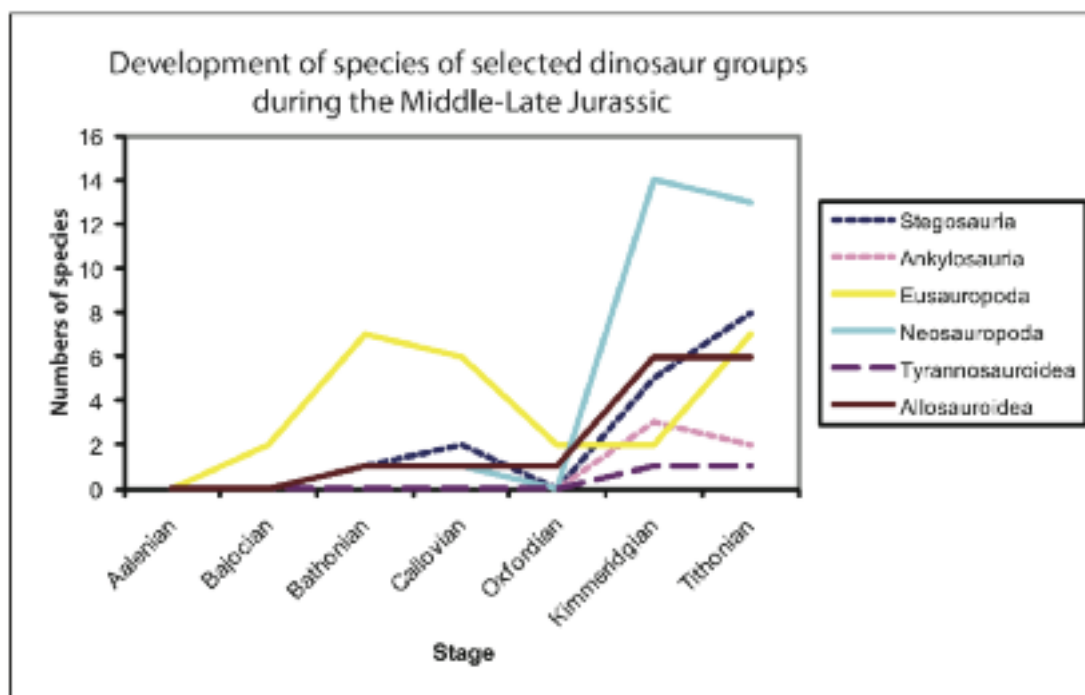


Figure 8 Numbers of species of several groups of dinosaurs during the Middle to Late Jurassic. Two from the ornithischians (*Stegosauria* and *Ankylosauria*); two theropods (*Tyrannosauroidae* and *Allosauroidae*); and two sauropods (*Eusauropoda* and *Neosauropoda*).

via Europe to the southern United States and Asia (Benton 1996; Upchurch *et al.* 2004). There is even a titanosaur tooth from Scotland (Barrett 2006), indicating that they had a foothold in Laurasia as early as the Middle Jurassic.

Discussion and conclusions

During the Early Jurassic, *c.* 200 million years ago, the CAMP lithospheric event was occurring along what was to become the line of the opening of the North Atlantic, producing vast amounts of lava. The CAMP could have been a barrier to faunal mixing between North American and eastern regions (Europe and Asia); however, the data do not appear to support this conclusion, as both regions have dinosaur taxa in common, such as basal thyreophorans and coelophysoideans. The main difference is that the prosauropodans appear to have died out in Europe, but not in North America. But absence of evidence may be a problem of collecting specimens rather than reflecting a real difference.

As the Middle Jurassic was the period of the opening of the Central Atlantic, it can be suggested that this had an influence on the speciation and extinction rates of dinosaurs. There are two peaks of increased numbers of dinosaur species in Laurasia (see Fig. 5B): one in the Bathonian (165–168 million years ago) and the other in the Kimmeridgian (151–156 million years ago). This represents an increase in dinosaur speciation occurring after the eastward (*c.* 170 million years ago), and the westward (*c.* 160 million years ago) ridge jumps in the Central Atlantic, respectively, as well as in the movement in the Yucatan block (*c.* 160 million years ago). At the Bathonian/Callovian boundary (*c.* 170 million years ago) there is a major carbonate productivity crisis in western Tethys due to a global marine transgression (Brigaud *et al.* 2009). There are also indications from the palaeoflora that conditions became more humid (Chamley 1989).

There are changes in the types of dinosaurs that are recognised prior to the Oxfordian dip to those after. Dryosaurs appear in the Kimmeridgian and most other ornithischians increase in numbers

of species. This may in part be due to changes in the modes of feeding of the herbivorous dinosaurs after the extinction of the prosauropods before the Bathonian (Buffetaut 2005), but also as a result of small extinctions opening up new niches driving speciation. Sauropods became the ‘high-browsers’ and other herbivores (ornithischians) the ‘low-browsers’ (Fastovsky and Smith 2004). The circum-Pacific volcanism at that time may have contributed to higher $p\text{CO}_2$ levels, leading to acidification (Brigaud *et al.* 2009).

The pre-Oxfordian extinction and post-Oxfordian speciation dinosaur events are also reflected in the marine realm. An increase in extinction rates for agglutinated foraminifera during the Callovian to Oxfordian (Kaminski *et al.* 2010), and a post-Oxfordian speciation is recorded in marine nannofossils (Roth 1987). There is no evidence for extraterrestrial bolide impacts at this time (MacLeod 1998), so this is unlikely to have been the cause. This effect also seems to be reflected in the dinosaurs of the southern continents (see Fig. 5A). The increased volcanism during this period combined with the opening and flooding of the Central Atlantic may have affected the levels of greenhouse gasses and well as producing partial barriers to faunas in both regions, and otherwise influenced the diversity of the dinosaur faunas of Laurasia and Gondwana. Whatever the cause, it appears that the extinction during the Callovian to Oxfordian had a global influence, as it can be recognised in Asia as well as in the circum-Atlantic region (Fig. 9, *overleaf*).

The Tithonian dinosaur extinction seems to have wiped out many of the species that developed during the Kimmeridgian and seems to be reflected in the evidence from the circum-Atlantic continents. This extinction is most noticeable at the species level (Figs 5, 6, 7, 8 and 9). Much discussion of this extinction has led researchers to conclude that it is not a significant extinction, because the dinosaur families persist across the Jurassic–Cretaceous boundary (Hallam and Wignall 1997). In terms of the numbers of species present in the Kimmeridgian

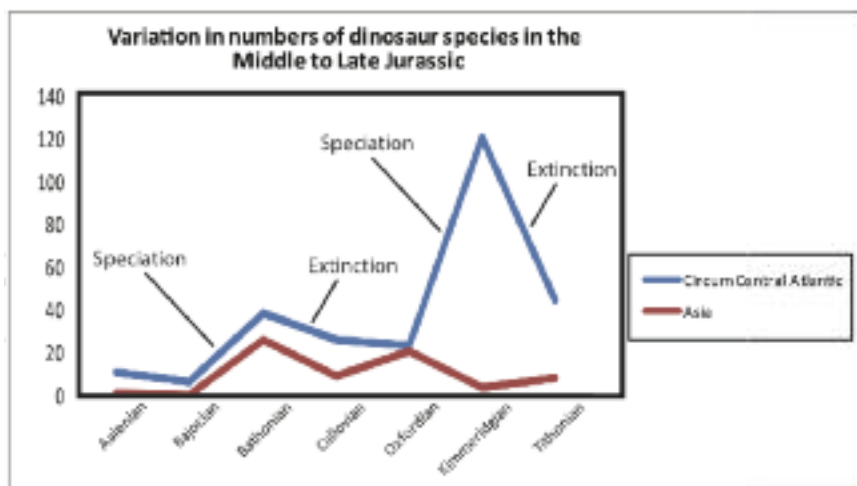


Figure 9 Variation in the numbers of dinosaur species in the Middle and Late Jurassic showing periods of speciation and extinction in the faunas close to the Central Atlantic as compared with the Asiatic faunas.

compared to the number in the Tithonian, there is certainly a significant change. The Tithonian extinction is a recognised extinction that affected the marine realm as well, although this appears to have been a regional, rather than a global, event (Hallam 1986; McCann 2008). This conclusion is supported by the dinosaur data where the Asian dinosaurs do not exhibit the same speciation and extinction profile in the Late Jurassic, despite following quite closely during the Middle Jurassic (Fig. 9).

The Serra Geral flood basalt eruption has often been quoted as the cause of the Tithonian extinction, but according to isotope dating, the eruption occurred somewhere between 120 and 130±5 million years ago just before the opening of the South Atlantic Ocean and well after the Tithonian extinction (Rampino and Stothers 1988). The timing of the Antarctic basaltic eruptions does seem to overlap with the whole of the Middle and Late Jurassic from *c.* 174±8 to 151±18 million years ago (Rampino and Stothers 1988), and hence may have had an influence on the extinction. There do appear to be some impact craters that coincide with the Tithonian extinction, but they are very small, only increasing in size and abundance later into the Cretaceous and hence are not thought to have had a significant contribution to the Tithonian extinction event (MacLeod 1998). The largest at this time is the Tookoonooka impact crater in Queensland, Australia, which is estimated to have been formed between 133 and 112 million years ago in the Early Cretaceous (it is about 60km in diameter, which is about a third of the size of the Chixulub crater that is thought to have contributed to the demise of the dinosaurs at the end of the Cretaceous) (Gorter 1998; Gostin and Therriault 1997).

Europe became an archipelago of islands in the Early Cretaceous. In this region some dinosaurs grew to about 10% of the weight of their relatives elsewhere (Benton 1996), perhaps in response to a gene-encoded response to environmental stress, such as limited food resources in a space-restricted area such as an island. Marine transgressions and continental drift split the dinosaur faunas, isolating them in the Late Cretaceous. Despite this, many groups still seem somehow to have been able to travel from Gondwana to Laurasia, despite the widening bodies of water between them, perhaps by some ephemeral landbridges. It was not only the titanosaurs — which previously existed in Scotland during the Middle Jurassic (Barrett 2006) — but also

the carnivorous abelisaurids that were able to travel across the Tethys Ocean to southern Europe (Benton 1996).

It is difficult to be certain of cause and effect when the margins of confidence of the isotopic dates for the volcanic rocks are greater than the length of some of the stages in the Jurassic. The dinosaur data are also limited by the number of species and specimens found; by the inherent problems of dealing with terrestrial deposits that are prone to erosion; and by the limitations of collecting large animals that require large excavation areas for one animal, compared to studying marine microfossils, which tend to occur in vast numbers in small samples. The precise dating of terrestrial rocks is also not as precise as the dating of marine rocks due to the lack of good zone fossils, unless there are some intercalated volcanic rocks. Having said that, there does appear to be some correlation between the various events

associated with the opening of the Central Atlantic, such as volcanic activity and marine transgressions, and changes in the numbers of dinosaur species. Endemism, speciation and extinctions of various dinosaur groups in both Laurasia and Gondwana correlate with the splitting of Pangaea as it progressed throughout the Mesozoic.

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